On the Organization of the Ornithosauria. By HARRY GOVIER SEELEY, F.L.S., F.Z.S., F.G.S., Professor of Geography in King's College, London.

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(PLATE XI.)

THE Pterodactyles have long been grouped with the Reptilia by the chief European anatomists. De Blainville placed them as a class between reptiles and birds. Earlier writers (Hunter and Blumenbach), with slender materials, included these animals with birds; and others, like Sömmerring, believed that they had some affinities to mammals. These conclusions necessitate modifications of the zoological ideas of reptile and bird on the part of those who would place Ornithosaurs in either group. But the evidence as to their organization has not been very conclusively set forth; and their place in nature has always been more assumed than proved. The difficulty consists chiefly in the absence from anatomical science of definitions which would fix the zoological value of the characters observed in such fossils as these. No one has specified with sufficient detail the osteological structures which constitute an animal a reptile, or a bird. The task is extremely difficult. My own endeavours that way have led to the conclusion that it is within the limits of possibility for an animal to have its skeletal characters so modified by loss, substitution, or development as to be no longer recognized as a member of its class by the form or proportions of a single bone. The great range of actual variations in the skeleton, seen among fishes, reptiles, and mammals, sufficiently demonstrates that characters must be found more constant than those of the bones before an extinct animal's affinities can be indubitably determined. Therefore, though ordinal groups are defined by the bones without difficulty, the characters of the class can only be found in the soft vital organs.

In the animals whose organization I purpose to examine, two of the vital organs can be investigated—one by the form of the cerebral cavity of the skull, the other by nearly all the bones showing conspicuous apertures which are formed and situate precisely as are the pneumatic foramina in the bones of birds. Such foramina characterize no other kind of skeleton; and since in birds they serve to prolong the air-cells from the lungs into the bones, it can only be inferred legitimately that the similar foramina in fossil bones subserved an identical purpose. The form of the cerebellum, the size and position of the cerebral hemispheres, and the inferior and lateral place of the optic lobes in the skulls of Pterodactyles offer another coincidence of distinctive structures with those of the class Aves. These are the only vital organs of birds which have a palæontological value: with them may be associated any bones that the conditions of existence tend to elaborate. Any corresponding conception of a reptile is unattainable; hence ideas of the boundaries of the Reptilia must always be vague.

Professor Huxley, in 1867*, so far modified the ordinary conception of a reptile as to maintain that the Ornithosauria were reptiles with hot blood. I had previously† detailed reasons for believing that they were hot-blooded, but had inferred for them from that an affinity with birds. It is within the limits of possibility for a reptile to be hot-blooded without having the organs associated with hot blood in mammals and birds, since there are hot-blooded fishes.

Professor Huxley followed up his belief that Ornithosaurs were hot-blooded reptiles by another belief that the pneumaticity of the bones and the avian characters of Ornithosaurs might be merely *adaptive modifications* ‡. By that expression Professor Huxley evidently intends to convey the impression that the structures in question are resemblances consequent upon the parts of the body having had to perform identical functions, so that the bones of different animals have acquired identical shapes and structures. For he goes on to say, "Pterodactyles, among reptiles, approach birds much as bats among mammals may be said to do. They are a sort of reptilian bat rather than links between reptiles and birds; and it is precisely in those organs—the manus and the pes—which in birds are the most characteristically ornithic, that they depart most widely from the ornithic type "‡.

I have given reasons for thinking neither manus nor pes the most characteristic organs of birds, and believe that brain and lungs are organs of incomparably greater value in questions of organization. When, therefore, Professor Huxley launches this scientific dictum without facts to support it, we may usefully compare his views as given at the Zoological Society. "Birds," says Professor Huxley, " have hot blood, a muscular valve in the right ventricle,

^{* &}quot;Classification of Birds," P. Z. S., 1867 p. 417.

[†] Ann. Nat. Hist. 1866.

[‡] Popular Science Review, 1868, p. 242, being a Royal-Institution lecture.

a single aortic arch, and remarkably modified respiratory organs; but it is, to say the least, highly probable that the Pterosauria, if not the Dinosauria, shared some of these characters with them. The amount of work involved in sustaining a Pterodactyle in the air would seem, physiologically, to necessitate proportional oxidation and evolution of waste products in the form of carbonic acid. If so, a proportional quantity of heat must have been evolved, and there must have been a ready means of eliminating the carbonic acid from the blood. We know of no such means except those which are afforded by highly developed circulatory and respiratory organs; and therefore it is highly probable that the Pterodactyles had more perfect organs of this kind than their congeners, accompanied by the correlative hot blood. But since we know that the organs of respiration and circulation of a bat are very different from those of a bird, it is quite possible that those of a Pterodactyle may have been different, in detail, from either "*.

This passage may perhaps be reconciled with the preceding one by means of the dictum often laid down by Professor Huxley, that birds are greatly modified reptiles. But I do not think that the assertion that birds are reptiles would go a great way towards aendering it probable that the pneumatic skeleton of Pterodactyles is an adaptive modification.

On the hypothesis that Pterodactyles are reptiles, Professor Huxley would infer, I think, that flight caused the development in them of the pneumatic skeleton; but seeing that the Cheiroptera, among mammals, have great powers of flight without the skeleton being pneumatic, the statement can but rank as a surmise unsupported by evidence, and, so far, contrary to evidence. Until some living animal, demonstrably reptilian, is discovered to possess limb-bones marked with pneumatic foramina, it seems to me that teaching from any one will lack weight when it refers fossil pneumatic skeletons to the Reptilia. Among living animals the pneumatic foramina exist only that avian lungs may have their air-cells prolonged into the bones; so that no other function can fairly be inferred for them when they are found in fossil bones.

The pneumatic foramina of Ornithosaurs so closely resemble those of birds in almost every bone of the skeleton, that the resemblance often amounts to complete coincidence. The holes are usually in exactly the same positions on each of the bones in both groups; and in both they have the same details of reticulate structure. It must, then, be sound physiology to infer that such

P. Z. S. 1867, pp. 417-18.

identity of structure is due to identical causation, unless we have at least some evidence to the contrary. If the formula *adaptive modification* means that the Pterodactyles acquired by flight lungs similar to those of birds, it seems as though it were only another and less striking way of saying that reptiles are birds. If Professor Huxley could give to reptiles a bird-like heart and birdlike lungs, it would be important to learn the characters by which they could still be recognized as members of the class Reptilia.

The only remaining vital character which can be recognized in a fossil is the brain; and if the respiratory system of a reptile could become adapted so as to be undistinguishable from that of a bird, what reason is there that it should not be supposed that the brain also of a flying reptile would become indistinguishable from that of a bird?

But between birds and Ornithosaurs there is a great structural resemblance in the brain. A bird's brain so fills its braincase that a mould of this chamber gives a true idea of the form of the brain. The evidence for the identity of cerebral structure in these two groups rests upon the form of the cerebral hemispheres in the *Pterodactylus longirostris* and on other specimens from the lithographic slate, on an undescribed skeleton from the Wealden of the Isle of Wight, preserved in the collection of the Rev. W. Darwin Fox, and on several fragments showing different portions of the brain-cavity of the *Ornithocheirus* in the Cambridge Upper Greensand. That these latter fossils do not pertain to true birds, remains of which also occur in the deposit, but really belong to Ornithosaurs, is demonstrated by the association of the similar Wealden cranium with a typical Pterodactyle skeleton.

The Upper-Greensand specimens on which I rely for evidence as to cerebral characters are two in number—first, the hinder part of a cranium, and, secondly, a mould of the upper portion of the brain-cavity. The former specimen is in the Woodwardian Museum of the University of Cambridge, and the latter in that of J. F. Walker, Esq., M.A., F.L.S. The Woodwardian specimen shows a vertical section of the brain made in about the line of junction of the frontal with the parietal bones, or just behind that line (Pl. XI. fig. 4). I have excavated the brain-cavity a little, so as to make its outlines distinct; but the hard and brittle character of the specimen rendered it impossible to remove the material which fills it. In its greatest lateral width it measures $\frac{15}{46}$ of an inch, while its greatest depth in the middle of each cerebral hemisphere is about $\frac{11}{16}$ of an inch. It has the outline shown in Pl. XI. fig. 4. I regard the upper part of the outline as showing that the cerebral hemispheres were divided from each other, as among birds, by a deep impression of the parietal bones. that they were convex from within outward, and deep from above downward, as among birds. At the two lower corners of the section of the cerebrum are two distinct rounded cerebral masses which extend outward beyond the adjacent part of the cerebrum, so as almost to excavate a way through the region of the alisphenoid bones (fig. 4, o). The position of these masses below the cerebrum and in the alisphenoids seems to me to demonstrate that they are the optic lobes of the brain; and since they hold the same position and proportion as the excavations for the optic lobes of the brain in the skulls of birds, I infer that in this important point the Ornithosaurian brain is identical with the avian brain. To make this clear, I have prepared a vertical section of the cerebral cavity in the skull of an owl in the same relative plane with the section of the fossil skull, and give the figure for comparison (see diagram, Pl. XI. fig. 5)-from which it will be seen that the only difference between them is, that the owl's brain has a wider cerebrum, and is marked by lateral cerebral impressions which are not shown in the fossil. These differences are only of the kind which distinguish the brains of different genera of birds from each other.

Mr. Walker's fossil displays the upper surface of the cerebrum (Pl, XI, fig. 2), and, so far as regards the form of the cerebrum, confirms the evidence from the Woodwardian fossil; but too little of the under part of the specimen is preserved for it to show the optic lobes. The cerebral lobes are $\frac{10}{16}$ of an inch long, and each is $\frac{7}{16}$ of an inch wide : they have the lateral outline rounded, and the front outlines combined in the middle to make the front of the brain rounded. The lateral outlines similarly converge behind, except that in between the hinder mesial part of the cerebral hemispheres is placed a distinct, small, convex, cerebral mass (Pl. XI. fig. 2, cm). It is separated from the cerebral lobes by well-marked grooves directed backward and outward, and does not extend between them for more than $\frac{1}{16}$ inch. In a line with the hinder limit of the cerebral lobes this mass attains its greatest width of about $\frac{5}{1.6}$ inch; and behind this line the cerebral mass becomes a little narrower. The outermost corners of this mass are each prolonged as a slightly elevated ridge obliquely outward and forward over the cerebral lobes towards the portion of the frontal bone which formed the hinder wall of the orbit. The antero-posterior extent of this cerebral mass (as preserved; for it is somewhat fractured behind) is $\frac{3}{16}$ inch; but on the under side of the fossil (Pl. XI. fig. 3, cm), where this brain-region is well defined between the bones on each side of it (fig. 3, s), it is $\frac{4}{16}$ inch wide, and extends forward for $\frac{7}{16}$ inch, thus demonstrating that while it is seen for $\frac{3}{16}$ inch behind the cerebrum, it also extends forward under the cerebrum for $\frac{4}{16}$ inch. Therefore I identify this cerebral mass as the cerebellum, and infer from the anteroposterior convexity of its exposed superior portion that its hinder outline was vertical, and did not extend much behind the part of the brain preserved. The ridge over the cerebrum is due to a blood-vessel.

The resemblance of form and arrangement of parts between this fossil animal's brain and the brain of a bird (Pl. XI. fig. 1) amounts, as far as the evidence goes, to absolute identity. This is manifest on comparing a cast of the brain-cavity of a bird with the natural mould of the brain-cavity of the Cambridge Greensand Pterodactyle. The cerebrum being the cerebrum of a bird, the optic lobes those of a bird, and the cerebellum that of a bird, no more perfect specimen could add to the force of the conclusion that the Ornithosaurian brain is an avian brain of typical structure. It seems to me, therefore, an inevitable conclusion that the Ornithosauria are members of the same great class as birds, and are separated from carinate and other birds only by such characters as divide mammalian or reptilian orders of animals from each other-that is to say, by modification of the skeleton. If this claim to admit the Ornithosauria, on account of vital structures, into the class Aves is allowed, then it follows that the skeletal modifications of Ornithosaurians are as much avian structures as the skeletal modifications of the Cetacea, Carniyora, and Monotremata are all mammalian structures.

Turning to the skeleton in Ornithosaurian animals, I propose to point out the characters of the several bones without regard to theoretical conception of the Ornithosaurian organization. On *a priori* grounds it would be reasonable to expect that no greater variations from a common avian plan would be presented than are seen in the variations from the mammalian common plan shown by Edentates, bats, and whales, or are presented by the variations of the several orders of reptiles from the common plan of the Reptilia. I do not think it will be found that the variations from the avian type of structure exhibited by the skeletons of Pterodactyles are as important as those in the cases cited have been.

First, as to the structure of the skull and vertebral column. Von Meyer has remarked on the preponderating resemblance to the bird's skull shown in the skulls of Ornithosaurian fossils from the lithographic slate of Germany; and elsewhere I have translated his exposition of their characters^{*}. But although he states the several bones, as well as their texture, condition, and arrangement, to be avian, he does not mention the particular birds with which comparison may be made. Some of these comparisons I will supply.

If our attention is turned to the skull, seen from above, as in the published figures and casts of *Rhamphorhynchus Gemmingi*, the outline of the skull is a long triangle terminating sharply in front, similar to that presented by the skull of the great African Kingfisher (*Ceryle maxima*), in which the positions and proportions of nares, orbits, and temporal fossæ correspond closely, the differences being that the Ornithosaur has no premaxillary facial joint, and the bird has no complete temporal fossa. The common Heron (*Ardea cinerea*) also resembles the Pterodactyle in the fore part of the head, but behind the eyes it has the skull both longer and larger.

If the comparison is made from the side view, the small backwardly placed nares and complete orbit of *Rhamphorhynchus Gemmingi* show some resemblance to these organs in the parrots. The orbital circle, however, is formed in different ways. An interesting resemblance, both in the position and proportion of the several regions of the side of the skull (nares, orbits, cerebral space and quadrate bone), may be noticed on comparing *Pterodactylus longirostris* and *P. scolopaciceps* with the Bar-tailed Godwit (*Limosa lapponica*). The quadrate bone is similarly inclined forward in the Curlew, Snipe, and other birds, while it articulates inferiorly with the squamosal region of the brain-case, as the quadrate bone articulates in birds and in no other animals.

When a bird has a circular orbit for the eye, the circle appears to be completed below by a downward and backward growth of the lachrymal bone uniting with a forward growth of the frontal bone in its postfrontal region. Many water-birds, especially the Maned Goose (*Bernicla jubata*), the Swan, and the Teal, show an approximation to such a condition. The Great Bustard, too, shows

^{*} Ann. Nat. Hist. 1871.

forward growths both from the squamosal and frontal margins; and in the Snipe both of these processes meet the lachrymal bone. Thus one distinctive feature of the bird's orbit, by which it differs alike from Ornithosaurs, reptiles, and mammals, is that it forms a circle above the bar containing the malar bone, so that the malar bone is not admitted into the orbit of the eye.

In the Ground-Hornbill (Bucorvus abyssinicus), however, and in the Shoebill (Baleniceps rex), the lachrymal bone meets the malar bar without uniting with it, and the postfrontal region of the skull is prolonged downward almost as far as the malar bar—thus showing that it is possible for a bird to have its orbital circle formed by the same bones, and in the same way, as among Pterodactyles: that is, the frontal bone is above, the lachrymal in front, and the malar below. But Ornithosaurs sometimes differ from birds in admitting the quadrato-jugal bone into the orbital circle behind. The quadrato-jugal bone has, I believe, in most specimens hitherto been regarded by others and by myself as the postfrontal bone; but the postfrontal bone seems to me now usually to have no separate existence in Ornithosaurs, being united with the frontal bone as in adult birds.

My reasons for making this determination are, that the bone in question appears usually to have two articulations with the quadrate bone, and to be situated between the malar bone and the proximal end of the quadrate bone. Since the frontal bone expands at the back of the orbit as in birds, and the squamosal bone similarly contributes to the wall of the brain-cavity, there can be no reason for supposing that the bone in question, which makes the outer boundary of the temporal fossa, is the postfrontal, so long as the quadrato-jugal bone remains unaccounted for. The position of the bone is somewhat analogous to that of the quadrato-jugal Hatteria, so far as concerns the orbit, and similar to the quadrato-jugal in Iquana in its relations to the quadrate and squamosal bones, and therefore is more lizard-like than the quadrato-jugal of birds. But, in consequence of this arrangement, it results that the malar bone unites with the distal end of the quadrate bone; and this union distinguishes Ornithosaurs from all existing animals, whether birds or reptiles. These differences from birds, even from a morphological point of view, ought not to be regarded as resemblances towards one class of animals or another, but merely as characters useful in the subordinate details of classification.

No ornithosaurian fossil has displayed the undisturbed palatal aspect of the skull; but in *Cycnorhamphus suevicus* and *Pachyrhamphus crassirostris* the palatal bones may be detected as slender elements comparable to those of birds. The palate of *Pachyrhamphus* may have approximated towards the palate of such a struthious bird as the Emu; but *Cycnorhamphus* had a palate more like that of a natatorial or gallinaceous bird, as I have already tried to show in a published restoration *. In neither of these genera, nor in any known Ornithosaur, have the palatal bones any reptilian features.

Formerly considerable weight was given to the occurrence of teeth in Ornithosaurians as a point of resemblance to reptiles ; but this feature is now balanced by the occurrence of similar teeth, according to Professor Marsh, in the jaws of the cretaceous birds Hesperornis regalis and Ichthyornis dispart, as well as by the presence of teeth anchylosed to the jaw in Odontopteryx ‡. Since Hesperornis possesses so many of the characters of existing birds, there seems to be no reason why the occurrence of teeth in Pterodactyles should be regarded as a character more reptilian than avian. Some years ago I pointed out that since the teeth in the maxillary bone in the Delphinidæ are all simple and conical with one fang, the occurrence of teeth similarly simple in Ornithosaurians is no more a resemblance to reptiles than it is to mammals, and is therefore valueless as a mark of affinity. The tooth-structure is not very like that of any living animal.

When printing my book on the Ornithosaurians, I stated that the teeth resembled those of some mammals in the dentinal cells. The point always appeared to require further examination; and beautiful new sections made for me by Mr. Cuttell, of New Compton Street, demonstrate no such structure. From studies of sections of teeth, it seems to me that we can by no means certainly determine, on microscopical evidence, whether a tooth is reptilian or mammalian, especially when the type to which it belonged is extinct.

In longitudinal sections of the tooth of *Ornithocheirus* from fang to crown (Pl. XI. fig. 11) the calcigerous tubes radiate as in the teeth of Ichthyosaurs and Plesiosaurs; they are wavy tubes which occasionally bifurcate, but are remarkable for the many branches

* Ann. Nat. Hist. 1871, vol. vii. pl. 2.

† Am. Jour. Sci. vol. x. 1875, pl. 10.

‡ Quart. Journ. Geol. Soc. vol. xxix. pl. xvi.

which each gives off at right angles. The branches appear to be best seen in the transverse section, where many can be traced extending in a wavy course for some distance at right angles to the tube from which they are given off. The branches are sometimes as large as the principal tubes, which, towards the outer part of the tooth run straight. In the transverse section (Pl. XI. fig. 12) the branches appear to unite the tubes together much as the principal tubes are united in some Carboniferous species of the coral Syringopora; but this appearance is probably delusive. The enamel is very thin, and only distinguished from the dentine by being perfectly translucent; but calcigerous tubes are continued into it without any break. Exactly the same kind of structure has not been figured, so far as I know, in any existing animal. It reminds me of that attributed by Professor Owen to Saurocephalus; but in this fish, which has a similar form of tooth, the tubes are fewer beyond comparison. Among reptiles, there is a resemblance in the number of tubes to Iguana. Cetaceans and bats indicate structural resemblances probably as close, though in those animals the tubes are fewer.

The only remaining points of importance in the skull are that the eyes usually, if not always, abut against the anterior walls of the brain-case, as they do in some birds, and that the skull is articulated at right angles to the vertebral column, as it is in all birds. Perhaps little importance should be attached to this latter character, although it is found in no reptile, because in Cetaceans the head is in a line with the vertebral column, as it is in reptiles, while in the fish *Hippocampus* the head is placed at an angle to the vertebral column, as it is in birds.

Finally, every point of the Ornithosaurian skull upon which I have not offered comment presents absolute identity with the corresponding structures in birds. I now pass them over, not because their great weight should be overlooked in an attempt to estimate the osteology of the group, but because there are no new facts to be adduced in addition to those given in previous writings on the subject.

On the whole, I do not regard the Pterodactyle's skull as differing from the bird's skull to any thing like the same extent as the skulls of birds, or of Pterodactyles, differ from each other.

The vertebral column presents considerable variety in the Ornithosauria. Owing to the conditions of fossilization, the number of vertebræ in the several regions of the body is not easily determined. There appear to be usually seven or eight cervical vertebræ, which is fewer than is recorded in any bird, though the number is not more reptilian than mammalian. Sometimes the vertebræ are elongated, subcylindrical, and without conspicuous processes, as in *Pterodactylus longirostris*, and then they closely resemble in form the vertebræ in the neck of the Purple Heron. If there were any ground for comparing the animal, as a whole, with Terrapins, a certain parallelism would be remarked in the form of the neck-vertebræ of the two groups.

In other genera of Ornithosaurs from the lithographic slate, such as *Cycnorhamphus*, in *Dimorphodon* from the Lias, and in all the Ornithocheiroidea from the Cretaceous strata, the neck-vertebræ are large, broad from side to side, more or less flattened on the under face, and have the neural arch extending transversely beyond the centrum, as in *Bucorvus abyssinicus*. But birds, even raptorial birds, have a much smaller development of the neural spine. No reptile has a neck formed on this plan.

As yet, the nature of the articulation of the centrum in the vertebræ of most Ornithosaurs from the lithographic slate is unknown, though the condition is certainly not uniform. In the genera from the Cambridge Upper Greensand and the Chalk all the vertebræ have the centrum depressed ovately, concave in front, and convex behind. Some of the vertebræ of Dimorphodon have the same character. But the elongated caudal vertebræ of that genus, like similar vertebræ from the Oxford and Kimmeridge Clavs, have the articular ends of each centrum biconcave, as are the later caudal vertebræ in most Vertebrata. This procœlous character of the neck and back is at once a difference from all known birds. and a resemblance to the form of vertebral articulation among lizards, serpents, and crocodiles. The resemblance is the more worthy of being carefully weighed, because no mammals are reported to possess proceduus vertebræ. Although, no doubt, a biconcave vertebra, such as that of Ichthyornis, or of the tail of an existing bird, might become as easily moulded to the lacertilian as to the avian form, hitherto the condition has not occurred in birds, recent or fossil; but on that account the probability of its occurrence hereafter is not decreased.

Nevertheless the character can scarcely be called reptilian, since in such reptiles as the Chelonians and Rhynchocephala for example other modes of vertebral articulation prevail. If the character is reptilian it must be a resemblance to either crocodiles, lizards, or serpents, but can only be so regarded provided the predominant resemblances of the skeleton prove to be with those ordinal groups.

The Ornithosaurian vertebræ, however, show a resemblance to those of birds and many mammals in the small size of the centrum and in the large extent to which the sides of the neural arch contribute to form the lateral parts of the intervertebral articulation. I have not detected a like structural condition in the vertebræ of reptiles. But the character becomes modified in importance by the relation being reversed in some mammals, since the canal for the spinal cord is sometimes partly formed by the centrum in Cetacea.

The atlas and axis resemble those of a bird in proportion and form; but the condition of the odontoid process is different. When the atlas separates from the axis of a bird, the odontoid process is seen usually, if not always, to have formed the upper part of the cup for the occipital condyle. In *Ornithocheirus* a perfect disk comes away from the axis, and displays a slight prominence on the upper part of the anterior face of the axis with a concave space around it. But I have no evidence whether the elevation represents the centrum of the atlas in a diminished form, or whether that bone unites with the other elements of the first vertebra, after the pattern of *Plesiosaurus* and *Ichthyosaurus*, as would seem not improbable. It thus differs alike from birds and reptiles.

Von Meyer states that the dorsal vertebræ vary in number from 12 to 16; but in associated sets of bones from the Cambridge Greensand the dorsal vertebræ are few. They resemble those of a bird in relative shortness, but do not appear to form a transverse platform from which the neural spine rises, as do similar vertebræ of adult birds and crocodiles, in this respect being more like vertebræ of lizards.

Sometimes the centrum is flat on the visceral side, as in *Apteryx*, sometimes rounded, as in such birds as the Heron. Altogether the dorsal region is less bird-like than is the neck, but the divergences do not show marked resemblances to any existing ordinal group of reptiles.

The nature of the attachment of the ribs may perhaps be variable. Several forms certainly possessed double-headed ribs like those of birds and mammals; and all specimens and figures, including

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those of *Pachyrhamphus crassirostris*, appear to me to demonstrate that the articulation of the ribs was avian, and not crocodilian.

The sacrum differs from that of a bird chiefly in its shortness, and in including but few vertebræ. Prof. Huxley has proposed to call the five posterior vertebræ of the sacrum in a chicken caudal, limiting the term "sacral" to the five vertebræ anterior to these, while the four vertebræ anterior to the latter are named dorso-lumbar.

The number of the vertebræ is variable in these regions, and they often differ slightly on the two sides of the animal. While such division on homological grounds is valuable, on morphological grounds it is untenable, since at no period of the development of the chick do the vertebræ named caudal and dorso-lumbar form part of either the tail or back.

The points stated by Prof. Huxley serve to show probable limits of variation among fossil birds, and that animals may be avian in having only four or five vertebræ in the sacrum; although they would then probably belong to a new subdivision of the bird class. In several Ornithosaurs there are four, five, or six vertebræ in the sacrum, so that the number of vertebræ is so far in harmony with the avian type as conceived by Professor Huxley. In having the neural spine well developed there is a resemblance to the anterior part of the avian sacrum, while in having the transverse processes well developed, there is a resemblance to the hinder part of the avian sacrum. The sacrum is therefore distinct from that of birds, and yet altogether unlike the sacrum of any reptile.

The caudal vertebræ vary considerably in Ornithosaurs. All the members of the Cretaceous order Ornithochelroidea apparently have elongated caudal vertebræ unlike those of existing birds, and resemble the anterior caudal vertebræ of reptiles in having the centrum concave in front and convex behind. But, so far as I am aware, in all the other forms (the PTERODACTYLIA) the caudal vertebræ, whether short as in *Pterodactylus*, or long as in *Rhamphorhynchus*, have the centrum flat or slightly concave at both ends.

In some birds the caudal vertebræ often present a marked resemblance in proportion and form of the articular face to those of *Plesiosawrus* and occasionally in Ornithosaurs the tail may have avian proportions. But the neural arch is never so elevated as in Birds, even when it is preserved; for in some specimens from the lithographic slate the neural arch in the tail is said to be absent, as it is in the later caudal vertebræ of mammals.

Thus it appears that the vertebral column shows some striking

resemblances to certain groups of reptiles, especially in the form of the intervertebral articulation; but this structure is coupled with so many other characters (especially in the neck and sacrum) which are not found in reptiles, that, unless the predominant resemblances of the rest of the skeleton prove to be with the Reptilia, it would be philosophical to infer that other groups of animals besides reptiles possess procedous vertebre. We have already seen that opisthocælian vertebræ occur in every division of the vertebrata; and this fact, when considered in connexion with the variations of intervertebral characters in different vertebrate classes, would appear to render the procedous articulation less important than it has been supposed to be by morphological anatomists.

The pectoral and sternal bones are about as markedly avian as is the skull. The sternum appears to differ from that of most birds in being as broad as long, while it is probably relatively much shorter. The keel is only well developed at the proximal end as in the Gannet; and the semicircular posterior border to the bone, observable in some German specimens of Ornithosaurs, is a character not seen in birds. Von Meyer reports, in some specimens of Rhamphorhynchus, that the lateral portions of the sternum to which the sternal ribs are attached are distinct ossifications, as they are in at least some young birds, such as the chicken. The sternal ribs which articulate with the sternum are ossified, as is the case with birds; and there is a resemblance to birds in that only a few join the sternum. But there is a striking difference from birds in that, behind the sternum, V-shaped abdominal ribs are freely developed, as in Hatteria &c., and these structures do not occur in birds. I have moreover never seen in an Ornithosaur any trace of the epipleural element characteristic of Hatteria, of Crocodiles, and of Chelonians. and so often seen in the ribs of birds; so that, if developed, it must have been cartilaginous.

The right angle at which the coracoid meets the scapula is characteristic of carinate birds. The coracoid much resembles the bone in birds, yet has distinctive differences. The bird-like features are the elongated form, rounded inner side, and compressed outer margin of the bone; the distal articulation with the sternum is concave from within outward, and convex from before backward, as in birds; and the proximal articulation with the scapula similarly looks backward. But there is a difference, in Cretaceous species, from the coracoid of a bird in that the bone is not prolonged proximally beyond the articulation for the humerus. With that character necessarily follows the absence of a furcula, seeing that there is no surface on the coracoid to which it might be attached.

In the so-called *Rhamphorhynchus Bucklandi*, and apparently in *Dimorphodon*, this clavicular process of the coracoid is developed, though perhaps a clavicle may not be inferred for those genera. The scapula is a bone which, in *Dimorphodon*, is compressed and curved like the scapula of the fowl, and was similarly placed. In the Oolitic fossils the bone is still more like the scapula of a bird than any thing else; but in the Cambridge-Greensand genera the form of the bone is subcylindrical, terminating backward in an expanded and abruptly truncated and ovate end. This is not bird-like, and not like the bone in any other animal.

The only reptiles which have the pectoral arch similarly consisting of scapula and coracoid are crocodiles and chameleons. Since the scapula is elongated in *Chamæleo* as well as in the Mole (*Talpa*), the elongation is evidently not correlated exclusively with development of the pectoral muscles. And since the coracoid has no corresponding form or function in bats, the shape of that bone in Pterodactyles cannot be explained by its function only. The Ornithosaurian humerus, with marked resemblances to birds and chameleons, is yet so different as not to be mistaken for either. Remembering that Ornithosaurs were often quadrupedal, and that the whole fore limb was usually modified for walking as well as for flight, it is scarcely to be expected that the resemblances of limbbones to those of any existing mammals should be remarkable.

In the forearm both bones are large and usually of equal size, as Von Meyer and Professor Owen long since pointed out; so that the ulna is as large as in a bird, and the radius much larger. The ulna is large in birds, I presume, because the feathers are attached along its shaft, and the equality in size of the bones in Pterodactyles may indicate that both bones performed nearly equal amounts of work. Still the resemblances to birds are more marked than to other animals. There is, however, in many species a third bone in the forearm, which is articulated to the pisiform bone. It is imperfectly developed proximally, and appears to correspond to the olecranon seen in the skeleton of Ophthalmosaurus. In Cycnorhamphus a second bone of this kind appears to be present, the homology of which is more difficult to understand.

The carpus has always been regarded as reptilian, seemingly because it consists of two rows of bones. It is a very variable part of the Ornithosaurian skeleton. In 1870, in my "Remarks on Prof. Owen's Monograph on *Dimorphodon*," I pointed out that in the Cretaceous genus *Ornithocheirus* (Pl. XI. fig. 6), the carpus consists of three bones :—a proximal carpal, as in birds, which corresponds closely in form with the bone in the ostrich (Pl. XI. fig. 7); a lateral carpal, as in birds, which I interpreted as the pisiform bone; while the third bone or distal carpal of *Ornithocheirus* is, in birds, of the same form, but becomes anchylosed to the metacarpus. Until placed in separate genera by me*, the Cambridge-Greensand fossils had been included by Prof. Owen in the genus *Pterodactylus*. Prof. Owen now, however, in recent publications of the Palæontographical Society, adopts the generic groups which I suggested, but discards my names, alleging that there is no evidence of avian type of carpus to justify the name of *Ornithocheirus*.

If the foregoing account of the carpus does not justify the name, I might quote Dr. Rosenberg's observations +, that in early life there are two elements in the distal carpal row of birds, and that these carpal bones subsequently unite with each other. Thev correspond with the four metacarpal bones of birds, and become subsequently united to the metacarpus. Thus in the composite structure of the carpus and in the number of metacarpal elements there is an absolute agreement with the conditions in embryonic or young birds, while I am aware of no such resemblances to reptiles. If the fourth metacarpal of the bird becomes absorbed, then Ornithocheirus apparently agrees with birds in having three metacarpal bones. But it differs from birds in the distal carpal (which is separated from the metacarpus) being made up of three carpal elements, one corresponding to each of the three metacarpal bones-although in the mature animal the metacarpals are not always attached to their corresponding carpal ossifications. The distal carpal bone of Crnithocheirus sometimes shows on its proximal surface a Y-shaped groove; and occasionally the sutural surfaces indicated by this groove remain unattached to each other. Hence the bones are placed one above the fork of the Y, and one on each side of its stem; so that they are not arranged in one line, as is usual, but in two lines. These three bones are probably the trapezoid, the magnum, and the unciform (Pl. XI. fig.9). The middle bone of the Y, I regard as the magnum squeezed out from between the other two, as is the case with the same bone in the horse and

^{* &#}x27;Index to Secondary Reptilia,' &c., 1869, and 'Ornithosauria,' 1870.

[†] Quoted in Foster and Balfour's 'Embryology,' p. 175.

other animals in which the metacarpus is unusually modified. One of the two other bones terminates at the end in a rounded articular edge, which gives attachment to another bone, which for convenience may be named the lateral carpal; it is evidently homologous with the lateral carpal bone of birds, which is probably the pisiform bone. I am aware that Dr. Foster and Mr. Balfour regard that bone in birds as the united lunar and cuneiform bones. Whichever nomenclature should be preferred, all are agreed that it is attached to the exterior side of the distal carpal; and as it has the same articulation in Ornithocheirus, it follows that the element of the Ornithosaurian distal carpal to which it is attached is the unciform bone; and to this bone the minutest metacarpal bone is attached (Pl. XI, fig. 10). The other carpal element is therefore the trapezoid; and that bone will be seen to give attachment to the wing metacarpal bone. The structure of this carpal row, and the articular surfaces on its distal face, demonstrate that the great wing-finger of Ornithosaurs is not the fifth digit, or little finger, as stated by the older writers, but the middle finger, or index finger, as I first determined many years ago. This is a point of some importance, since it removes the Ornithosaurian hand from the category of osteological anomalies, and shows that it is constructed on a plan absolutely identical with the plan of the hand in birds; for it is the second or index digit in birds also which is chiefly extended for the support of the wing-membrane.

The distal carpal row of *Ornithocheirus* appears to differ from the corresponding bones in birds in being formed from three centres instead of two, though the rule is not constant for all Ornithosaurs; while, on the other hand, we have no evidence that the two distal carpal cartilages, detected by Dr. Rosenberg, characterize the distal carpal row of all birds. In any case we are justified in correlating the two carpal cartilages of the young bird with the existence of the two metacarpal bones of the adult which are anchylosed to them; while, since Pterodactyles have three or four metacarpal bones fully developed, we may expect to find a corresponding number of carpal elements in the distal row of the Ornithosaurian carpus.

I prefer to regard the lateral carpal as the pisiform bone, because it articulates proximally with a third bone of the forearm, which becomes intelligible as the distal end of the olecranon—an interpretation to which I am led by a study of certain Ichthyosaurs, regarding the olecranon as a third bone of the forearm, external in position to the ulna, and capable of being developed either proximally or distally. Whatever value may be attached to the resemblances of this carpus to the carpal bones of birds, it appears to render a modification necessary of Prof. Huxley's statement that the manus is a part of the skeleton in which birds and Pterodactyles diverge most widely.

Turning next to the metacarpus, I find that just as Dr. Rosenberg describes four metacarpal cartilages, as I also have observed in the chicken, so Pterodactyles from the Lithographic slate have four metacarpal bones-one of them more developed than in birds, and three thread-like, or at least much more slender than the other. The Ornithocheirus from the Cambridge Upper Greensand shows on the distal surface of the distal carpal three distinct articulations for metacarpal bones, two of which have articular surfaces of not dissimilar size ; and these seem to me to correspond to the two elongated metacarpal bones of birds. The fact of the metacarpal bones not being anchylosed together has never been thought to militate against the systematic position of Archæopteryx as a bird. Like the blended characters of the metatarsus in birds, it is so certainly functional that I am not disposed to regard the separate condition of the metacarpal bones either as a very important character, or as an evidence of reptilian affinity in Ornithosaurs. The Pterodactylian metacarpus, then, as Professor Owen has demonstrated, does not diverge greatly from the metacarpus of Archæopteryx.

The resemblance of the wing-digit to that of a bird is very remarkable, since the difference chiefly consists in the introduction of extra phalanges into the Ornithosaurian wing-finger.

There is felt by some writers to be a difficulty in accepting any modification of the old interpretation of the Ornithosaurian hand, on account of the number of phalanges in each of the four digits present in all Pterodactyles from the Oolitic rocks, though Von Meyer has said that the number of the phalangeal bones is variable in those animals. The number is usually stated as 4, 4, 3, 2; which, according to the interpretation of the hand just given, would read, four bones in Digit II., four in Digit III., three in Digit IV., and two in Digit V. So long as the Pterodactyle was supposed to be a modified lizard it was not unnatural that the reverse reading should be taken, and the increase in number of phalanges considered to be in harmony with the lizard type, in which the phalanges from first to fifth are 2, 3, 4, 5, 3; while in the chameleon they run, from first to fifth, 2, 3, 4, 4, 3. Thus, striking off the fifth digit of the chameleon, there looks to be an à priori probability that the number of phalanges, digit for digit, is identical with that in the digits of of the Ornithosaurian hand. Von Meyer appears to have suspected a fallacy in this conclusion ; for, in his ' Fauna der Vorwelt,' he observes, "even Cuvier believed that the wing-finger corresponded to the fourth finger of lizards; but lizards, like crocodiles, have five fingers, so there can be no real affinity." In this is a suggestion of explanation of the difficulty. If the animal were essentially a lizard, then it would be improbable that the lizard plan of the hand would be departed from, even when modified for flight. But if the animal is not a lizard, or even a modified lizard, then there can be no à priori reason for anticipating any structure of hand whatever. For though mammals usually have three phalanges in each digit, Cetacea are not to be classified by digital rules. If the Ornithosauria are admitted to be an extinct order either of reptile or bird type, then, bearing in mind the variation in the number of phalanges of the digits in existing reptile orders, I cannot realize any insuperable difficulty to believing that the phalanges of the second to fifth digits of chameleon, 3, 4, 4, 3, might under exceptional functional conditions become altered to the Ornithosaurian formula 4, 4, 3, 2. The matter of a phalange more or less in a digit in an extinct type is not the sort of evidence on which to settle an animal's place in nature, or on which to determine such homologies as those in question. The carpus is the only key to the structure of the hand. If that has been correctly interpreted in the Cambridge-Greensand Ornithocheirus, then the inferences which it enforces must, I consider, be true also for the other genera of Pterodactyles, no matter what the number of bones may be in their digits. In short, this portion of the skeleton diverges wider than any other from the bird and reptile types, and is distinctive of Ornithosaurs.

Thus, reviewing the morphological indications of the fore limb, and of its scapular arch, I fail to detect any characters which can be shown to be decidedly reptilian; nor do I detect, except in the ways pointed out, any remarkable divergence from birds; though the divergences are usually sufficient to prevent an experienced anatomist from mistaking even isolated Pterodactyle bones for the bones of birds. On the other hand, the whole limb in every part shows characters which are only found in the bones of birds, which I cannot see my way to explain as adaptive modifications, because bats, which similarly fly, have no such characters. The patagial membranes, which are well preserved in a specimen figured by. Winckler as *Pterodactylus Kochii*, prove to be exactly in the same regions as the patagial membranes of the wing of existing birds; while the great elongation of the wing-bones in Ornithosaurs only extends the wing to a similar extent to that in which the wing of a bird is extended by its feathers. It is reasonable therefore to suppose that if less organic energy were directed to formation of the covering for the skin in birds, more might go to the elongation of the wing-bones.

Finally, in the absence of any manner of evidence as to the existence of winged reptiles, and in face of the evidence as to avian resemblances which has been given, it seems to me hazardous to infer that the characters which some Pterodactyles may seem to have in common with reptiles in the bones which have been discussed, indicate any close genetic relation between the two types.

The pelvis and hind limb are the least reptilian portions of the Ornithosaur an skeleton. Whatever may be the physiological significance of the relation of direction of the ilium to the sacrum in the vertebrate classes, the morphological fact remains that in birds the ilium extends along the sacrum both in front of the acetabulum for the femur and behind it, and that this condition characterizes no other existing group of animals. In mammals and batrachians the ilium is directed forward, while in reptiles it usually directed backward or is vertical. And though the ilium of a seal makes an approximation to the ilium of a crocodile, which may be to some extent functional, these osteological characteristics of classes are sufficiently well marked to suggest the inference that an animal with the avian form of ilium is likely to be related to birds, either as an ancestral or as a parallel group. Like the whole pelvis the ilium is variable among Ornithosaurs; and in so far as it diverges from the avian form, it approximates to the mammalian shape. But it is rarely, if ever, so deep as in a bird, never has the characteristic avian form, terminates at both extremities in relatively narrow rounded processes, and is attached to sacral ribs which are longer than is usual among birds. There is also a remarkable difference from birds in the ilium joining the pubis and ischium in the middle of the acetabulum, which is thus made imperforate in the specimens which I have examined. This imperforate character is also found in reptiles. And though the ischium and pubis are occasionally directed backward after the LINN. JOURN .- ZOOLOGY, VOL. XIII. 10

manner of the Apteryx, the two bones are usually united by suture throughout their length, so as to leave a small obturator foramen near to the acetabular border. If this foramen were larger, the bones which enclose it would bear a close resemblance to those of the *Echidna*, which is the more interesting since, in common with the lower mammals, the Ornithosaurs also possess prepubic or marsupial bones. These bones are of different forms in the several groups of Ornithosaurs, being triangular in *Dimorphodon*, T-shaped in some genera from the Lithographic slate, and probably forming by union with each other a bow-shaped arch in another genus from Solenhofen.

The exact position of the prepubic bone on the anterior margin of the pubis is not quite certain, though probably placed in the middle of the margin; and there may be some doubt whether it is truly homologous with the marsupial bone. In Chelonians and Lacertilians a prepubic process is developed, often of large size, and the ornithosaurian bone may be likened to what such a process might become if converted into a distinct osseous element. A smaller but similar process is also to be seen on the pubic bone in some birds, such as the Apteryx, and in many mammals. In Iquanodon the process is enormous. The pelvis might perhaps as easily be regarded as of a modified mammalian type as avian; but it does not closely resemble either, and is somewhat intermediate between them. In this light it may serve to point a caution by showing that monotreme characters in the pelvis may coexist with lacertian characters in the articulations of the vertebræ. The pelvic bones met in the median line of the body, as in mammals and reptiles, and were not divided from each other, as is usual among birds.

The femur is in no respect a reptilian bone, unless it be in sometimes having the articular head directed a little forward. But in most English specimens there is a distinct articular head separated from the shaft of the bone by a considerable neck, which is directed upward as in carnivorous mammals; though in the genera from the lithographic slate the proximal end of the bone is more like the same part in birds. The distal end is rarely so deeply grooved in front as in the bird's femur, though it corresponds in thickness and form and does not approximate towards mammals.

The tibia and fibula are altogether avian, so much so that in many genera no anatomist could distinguish them from the same bones in birds. The fibula, slender, style-like, developed chiefly at the proximal end (Pl. XI. fig. 8, f), is often prolonged, no thicker than a thread, down the tibia to its distal end. The tibia expands moderately at the proximal end, is elongated, and terminates distally in a rounded trochlear end identical with that of birds, and apparently similarly formed by the anchylosed tarsal bone (Pl. XI. fig. 8, a). This may be seen in *Dimorphodon* (Pl. XI. fig. 8) and in many Ornithosaurs from Solenhofen, though the tarsal element is occasionally unanchylosed, as in young birds. This point has some interest, since the blending of the tibia and tarsus is one of the strongest points in Prof. Huxley's definition of a bird. And it seems to assist in modifying Prof. Huxley's assertion that the pes is a part of the skeleton in which birds and Ornithosaurs diverge most widely.

The metatarsal bones of Ornithosaurs are perhaps the most variable part of the skeleton. They appear to have been applied to the ground as in unguiculate mammals and reptiles, sometimes to have diverged widely, and sometimes to have been packed close together as in *Dimorphodon*. There is no evidence that they became anchylosed into one mass in any species; but, on the other hand, the evidence is not perfectly satisfactory that the metatarsal bones were anchylosed in *Archæopteryx*.

Ornithosaurs have either four or five toes, in which the phalanges appear usually to successively increase in number as in birds and lizards. The claws also are large and compressed from side to side as in lizards and birds.

Thus in the hind limb there is no structure which can be regarded as truly reptilian, though the separation of the metatarsal bones, taken together with the number of phalanges in the digits, is a closer resemblance to reptiles than to birds. But the partial separation of the metatarsals in the Penguins seems to indicate that total separation of the bones would not be inconsistent with avian structure.

From this review of the osteology of this group of animals, it seems to follow :---

(1) that the reptilian hypothesis of their structure, though not without some interesting indications, especially in the vertebral articulation, is in general so unsupported and so opposed to facts that it must be regarded as no longer tenable.

(2) That if the pneumatic foramina and cerebral structures had

remained unknown, the forms of the bones would have been sufficient to show that in their osteology Ornithosaurs resemble birds more closely than other animals; and that the differences from birds in osteology are much less than the differences between the several orders of mammals or of reptiles.

(3) That the resemblances to reptiles do not necessarily indicate genetic affinity with reptiles, any more than the resemblances to mammals indicate mammalian affinities; and that it is more than probable that both kinds of resemblances are to be ranked among the ordinal rather than with the class characters of the group.

(4) That the osteology, being largely avian, is in entire harmony with the indications of the soft organs, and justifies the conviction that the pneumatic foramina seen in the bones served identical purposes in living birds and in these animals, and therefore that Ornithosaurs form a group of birds which bears relation to existing birds such as the Chelonia hold to the Crocodilia among reptiles. That is, Pterodactyles are birds in the large sense of the term, in some respects much more reptilian than any birds which now survive.

Hereafter perhaps it may be found desirable to group Ornithosaurs with the Dinosauria and Dicynodontia in the class Palæosauria instituted by Von Meyer for those extinct orders which hold places intermediate between the higher vertebrata; but in the mean time they may well rest near to birds.

DESCRIPTION OF PLATE XI.

- Fig. 1. Brain of Owl (Strix otus), seen from above, after Leuret.
- Fig. 2. Natural mould of the upper part of the brain-cavity of an animal from the Cambridge Upper Greensand, referred to Ornithocheirus, showing the cerebellum (cm) between and behind the cerebral hemispheres. Portions of the cranial bones in the squamosal regions (s) are left attached to the mould. Nat. size.
- Fig. 3. Inferior aspect of the same specimen, showing the oblong mass of the cerebellum (cm) extending between (s) the lateral bones of the hinder part of the brain-case and (e) the back of the orbit of the eye. Nat. size.
- Fig. 4. Transverse vertical section through the parietal segment of the skull of an *Ornithocheirus* in the Woodwardian Museum, showing the position of the optic lobes (o) relatively to the cerebrum (c).
- Fig. 5. Transverse vertical section through the skull of an owl in the parietal region, for comparison with the preceding figure of an Ornithosau-

rian. In all these figures, c, cerebrum; o, optic lobe; cm, cerebellum; s, squamosal region.

- Fig. 6. Vertical diagram of the carpus of *Ornithocheirus*, for comparison with fig. 7.
- Fig. 7. Vertical diagram of the carpus of an Ostrich (*Struthio camelus*). In these figuers, *p*, lateral carpal; *q*, proximal carpal; *r*, distal carpal.
- Fig. 8. Tibia and fibula of *Dimorphodon* from the Lias, from a photograph of a specimen in the British Museum: t, tibia; f, fibula; a, anchylosed tarsal element. $\frac{3}{4}$ nat. size.
- Fig. 9. Diagram outline of proximal surface of distal carpal of Ornithocheirus, showing separation into:—m, magnum; td, trapezoid; u, unciform.
- Fig. 10. Diagram of distal surface of same distal carpal, showing pn, deep pneumatic foramen at the confluence of the three bones, and outlines of the positions of articular surfaces for three metacarpal bones. The evidence for these diagrams is in the Woodwardian Museum.
- Fig. 11. Longitudinal section of a tooth of *Ornithocheirus*, curved from end to end, showing close-set radiating calcigerous tubes. Enlarged $\frac{3}{4}$.
- Fig. 12. Transverse section from the base of the crown of a large tooth of Ornithocheirus from the Cambridge Upper Greensand. Enlarged 3.

Notes upon the Oxystomatous Crustacea. By EDWARD J. MIERS, Esq., F.L.S.

[Read June 15, 1876.]

(Abstract.)

In this paper (which will be published shortly in the Society's Transactions with illustrations) the author first enters into the literature of the subject, and then gives descriptions of species of the family Leucosidæ.

Of the genus *Leucosia* there are in the British Museum eight species hitherto unrecorded; and these are now named and may be enumerated as follows :---

L. fusco-maculata.	L. reticulata.
L. pulcherrima.	L. whitmeei.
L. affinis.	L. perryi.
L. brunnea.	L. pubescens.

A variety of *Myra mamillaris*, Bell, is noted, possibly an immature example; and he suggests that the *M. carinata* and *M. elegans* of Bell may turn out not to be adult animals.

Nursia sinuata is referred to as a new Australian form; and comparisons between what have been termed N. plicata, N. abbreviata, and N. hardwickii are instituted. Arcania granulosa and Cryptocnemius holdsworthi, respectively from Australia and Ceylon, are considered among the new species.

